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Total number of authors:
27

Published in:
Science

Link to article, DOI:
10.1126/science.aao1807

Publication date:
2017

Document Version
Peer reviewed version

Cite as: M. Sikora *et al.*, *Science* 10.1126/science.aao1807 (2017).

Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers

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Present-day hunter-gatherers (HGs) live in multilevel social groups essential to sustain a population structure characterized by limited levels of within-band relatedness and inbreeding. When these wider social networks evolved among HGs is unknown. Here, we investigate whether the contemporary HG strategy was already present in the Upper Paleolithic (UP), using complete genome sequences from Sunghir, a site dated to ~34 thousand years BP (kya) containing multiple anatomically modern human (AMH) individuals. We demonstrate that individuals at Sunghir derive from a population of small effective size, with limited kinship and levels of inbreeding similar to HG populations. Our findings suggest that UP social organization was similar to that of living HGs, with limited relatedness within residential groups embedded in a larger mating network.

Opportunities to investigate the population dynamics of early AMH populations are rare owing to a dearth of human remains, with wide variations in ancient population size estimates from ethnographic or archaeological data (*1*, *2*). In the absence of evidence for true contemporaneity among individuals recovered archaeologically, the population structure of foraging groups is even harder to establish. Exceptions are cases of multiple UP individuals buried simultaneously or originating from sufficiently close temporal and spatial proximity that they may represent a single social group.

One such example of multiple burials is Sunghir, a site harboring two of the most extraordinary UP burials known (*3*, *4*) (figs. S1 and S2 and tables S1 to S4): one of an adult male (Sunghir 1 [SI]), and another one of two sub-adults (Sunghir 2 and 3 [SII and SIII]), originally thought to be a boy and girl, interred head-to-head. All remains were covered in ochre, and accompanied by rich grave goods including ivory beads and spears, armbands and carvings, as well as arctic fox canines. Adjacent to SII was the femoral diaphysis of an adult (Sunghir 4 [SIV]) that had been polished, hollowed-out and filled with red ochre. The site also yielded other less complete human remains, some of uncertain stratigraphic provenance (Sunghir 5-9 [SV-SIX]). Radiocarbon analyses place the age of SI-SIV between 34.6 and 33.6 kya (*5*, *6*). The homogeneity in morphological traits (e.g., metopism) among the remains, as well as signs of possible congenital pathologies in SIII have been interpreted as evidence of inbreeding (*3*). Other UP individuals with reported congenital or degenerative pathologies (e.g., at Barma Grande and Dolní Věstonice) (*3*) reinforce the view that UP groups were small and susceptible to inbreeding, possibly

similar to what has been reported for the Altai Neanderthal (*7*). However, genomic data available for some of those individuals (*8*) were of insufficient coverage for inferring population sizes and inbreeding levels.

We screened six of the Sunghir individuals (SI-SV; Sunghir 6 [SVI]) to assess DNA preservation, five of which (excluding SV) yielded sufficient endogenous DNA for genome sequencing. We sequenced those genomes to an average depth-of-coverage ranging from 1.11X to 10.75X (figs. S3 and S4 and tables S5 and S6), and compared them to panels of modern and ancient human genomes (*4*). All individuals were genetically male on the basis of the fraction of Y chromosome reads (table S7), including SIII who was previously identified as female (*3*). Contamination levels from X chromosome heterozygosity were low (0.33% – 0.90%, table S5) except for SVI (13.1%). Radiocarbon dates indicate that while SV is only slightly more recent than the other individuals, SVI is from ~900 yBP (figs. S5 and S6 and tables S8 to S10). Together with mtDNA and Y-chromosome haplogroups (W3a1 and I2a1b2, respectively), these data indicate that SVI is not associated with the UP burials at the site, and was therefore excluded from further analyses.

Analyses of mtDNA genomes place SI-SIV in haplogroup U, consistent with West Eurasian and Siberian Paleolithic and Mesolithic genomes (*9*) (fig. S7 and table S5). SI belonged to haplogroup U8c; the sequences for the three individuals from the double burial (SII-SIV) were identical, and belonged to haplogroup U2, which is closely related to the UP Kostenki 12 (*8*) and Kostenki 14 (*10*) individuals. Phylogenetic analyses of the Y chromosome sequences place all Sunghir individuals in an early divergent lineage of haplogroup C1a2 (fig. S8 and tables S12 to S15). Y-chromosome haplogroup C1, which is rare among contemporary Eurasians, has been found in other early European individuals including the ~36 ky-old Kostenki 14 (*11*).

We investigated the degree of relatedness among the Sunghir individuals with a method that allows relationship inferences up to a third degree, but does not rely on allele frequencies (*4*). Surprisingly, none of them were closely related (that is, third degree or closer), despite the fact that the SII-SIV individuals buried together share both mitochondrial and Y-chromosome lineages (Fig. 1 and tables S16 to S23). We then inferred genomic segments that were identical-by-descent (IBD) and homozygous-by-descent (HBD) from three higher coverage Sunghir genomes (SII-SIV) and a panel of ancient and contemporary humans (*4*). We compared their distributions to those inferred from whole genomes obtained using coalescent simulations (*12*) of randomly mating populations with varying effective population sizes (N_E) (fig. S9). The distribution of HBD tracts were different between AMH and archaic humans, indicating small effective population sizes and/or recent inbreeding in archaic individuals, particularly the Altai Neanderthal (*7*, *13*) (Fig. 2A and figs. S10 to S14).

Patterns of pairwise IBD-sharing detect close genetic relatives in modern individuals (Fig. 2B). However, the Sunghir pairs do not share sufficiently long IBD tracts to suggest relatedness at the 1st or 2nd degree, consistent with the results from genome-wide identity-by-state (IBS) counts (Fig. 2B and fig. S15). Interestingly, the effective population sizes tended to be higher (N_E ~ 500) for two out of three Sunghir pairs than those estimated from HBD segments (N_E ~ 200). N_E from both HBD and IBD tracts (*4*) was within the range, or slightly higher, than that of contemporary non-African HG populations (Fig. 2C), particularly from genetically isolated groups (*14*).

Genetic clustering of ancient individuals using outgroup-f_3 statistics f_3(Mbuti; Ancient$_1$, Ancient$_2$) indicates shared genetic drift and tight clustering of the Sunghir individuals, which form a clade to the exclusion of all other individuals (Fig. 3, figs. S16 to S20, and tables S28 and S29). Furthermore, we find genetic affinities between the Sunghir individuals and those from Kostenki (12 and 14), as well as with the 'Vêstonice cluster' (*8*), associated with the UP Gravettian culture.

Individuals mapped onto a previously inferred admixture graph of early Eurasians (*4*, *8*) placed the Sunghir cluster as a descendent of a lineage related to the Kostenki 14 individual, contributing the major fraction of the ancestry of the 'Vêstonice cluster' (Fig. 3C and figs. S21 to S24). Adding the low coverage Kostenki 12 individual suggests a closer relationship to the Sunghir group rather than with the earlier Kostenki 14 individual (fig. S25). Finally, Kostenki 14 shows substantial population-specific drift after its divergence from the shared ancestor with Sunghir, allowing us to reject a direct ancestral relationship to both Sunghir and Kostenki 12 (fig. S26). These results suggest that the people at Kostenki were at least partially replaced by later groups related to Sunghir, which exhibit genetic affinities with individuals of the more western Gravettian culture.

Our high coverage Sunghir individual (SIII), allows us to explore quantitative models of Eurasian demographic history. Using coalescent-based modeling of the site frequency spectrum (SFS) (fig. S27), we estimate that SIII diverged ~38 kya (95% CI 35-43) from the lineage ancestral to contemporary Europeans, with a relatively small effective population size (N_e = 297; 95% CI 158-901) (Fig. 4A, figs. S28 and S29, and tables S24 and S25). The Ust'-Ishim genome, a 45 kya UP individual from Siberia (*15*) which diverged from the Asian lineage (~48 kya; 95% CI 45-55) soon after the initial divergence among Eurasians (~52.5 kya; 95% CI 49-57), indicates a comparably higher effective population size (Ne = 1,203; 95% CI 253-7098) (Fig. 4B, figs. S30 and S31, and tables S26 and S27). The best-fit models also suggest a

common Neanderthal admixture event shared by all Eurasians at 55 kya (95% CI 52-63), consistent with previous estimates (*11*, *15*). However, we also find evidence of multiple Neanderthal admixture events in both SIII (36 kya; 95% CI 34-42) and Ust'-Ishim (47 kya; 95% CI 44-51), the latter introgression providing an estimated 0.6% (95% CI 0.002-1.53) of Neanderthal ancestry to SIII. That excess may reflect either further pulses of Neanderthal introgression, or selection against Neanderthal introgressed regions in AMHs as previously suggested (*8*, *16*–*18*). Analyses of putative archaic-introgressed genomic segments (*4*) confirms a higher level of Neanderthal ancestry and a longer average Neanderthal segment length among UP individuals, in agreement with their closer proximity to the human-Neanderthal admixture event than present-day Eurasians (fig. S36). Assuming that the Sunghir individuals are contemporaneous (*4*), we obtain a refined estimate of the time since admixture at 770 generations (95% CI 755-786). Accounting for the uncertainty of both the admixture estimate and ^{14}C ages, this corresponds to an admixture date between the ancestors of Sunghir and Neanderthals between 53.6 and 58.1 kya (at 29 years/generation (*19*)), in agreement with the results obtained from coalescent modeling (fig. S37).

Our results suggest a social and population network of HG demes that preferentially mated within sub-groups, with exogamy and regular exchanges between demes. Among contemporary HGs, primary kin constitute <10% of residential groups, leading to low genetic relatedness (*20*, *21*). Some modern human groups exhibit increased levels of inbreeding, including populations where consanguineous marriage practices are encouraged, or geographically isolated HG groups such as those from the Amazon rainforest region (Fig. 2, A and C). In contrast, patterns of HBD among the UP individuals are consistent with randomly mating populations of moderate effective size (N_E ~ 200), suggesting that close consanguineous mating was avoided (Fig. 2, A and C). Although our findings are currently limited to a single UP site, if they are representative of early UP HGs more generally, they reveal a social structure and cultural practices that emphasized exogamy. This is consistent with archaeological evidence of high mobility in the UP (*22*), perhaps comparable to the scale of mobility seen ethnographically among small foraging bands at high-latitudes (*23*). We note that this interpretation relies on the evidence that all individuals at Sunghir were contemporaneous and members of the same social group. While this is clearly the case for the two children in the double burial (SII, SIII), it is possible that both SIV and SI were members of different social groups, potentially separated in time from SII and SIII. Nevertheless, the shared material culture, overlapping radiocarbon date intervals, as well as close genetic relationship among all individuals, all support this inference.

Although the number of ancient genomes available remains small, the differences in inbreeding levels, and thus group organization, between AMH groups in the UP and Neanderthals are intriguing. The small reproductive groups of UP AMH at Sunghir apparently avoided inbreeding and its deleterious consequences, in contrast to what has been observed for the Altai Neanderthals. We caution that more genomic data on Neanderthals from other regions is necessary to conclude whether the patterns observed in the Altai are representative of their genetic diversity more generally, or if that individual was an outlier. Assuming the former, whether this would reflect ongoing extinction of Neanderthals or a more general difference in social behavior and cultural practices also remains unknown. Our results nonetheless suggest that the human HG social structure of low levels of within-band relatedness, complex family residence patterns, relatively high individual mobility and multilevel social networks were already in place among UP societies 34 kya. This social structure may have affected the development of cooperation and information transfer that underlie the evolution of culture in humans (*20*, *21*, *24*, *25*), and may be crucial to understanding our species unique evolutionary resilience and trajectory.

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ACKNOWLEDGMENTS

P.R.N.'s research was funded by the FP7 Marie Curie program (CIG Nr 322261), Isaac Newton Trust, Leakey Foundation, and McDonald Grants and Awards Fund. DMB's research was funded by the H2020 Marie Skłodowska Curie program (EF Nr 656325). ID and VS were supported by a Swiss NSF grant 31003A-143393 to LE. GeoGenetics is supported by the Lundbeck Foundation and the Danish National Research Foundation (Grant DNRF94), and KU2016. V.V.P., E.Y.P., and P.A.N. are supported by Russian Science Foundation project N 16-18-10265-RNF. AM was supported by ERC Consolidator Grant 647787-LocalAdaptation. Thanks to L. Moreau, A. Sinistyn for helpful discussions. We thank the staff of the Danish National High-Throughput DNA Sequencing Centre and the laboratory technicians of the Centre for GeoGenetics for technical assistance. Genomic data are available for download at the ENA (European Nucleotide Archive) with the accession number PRJEB22592

SUPPLEMENTARY MATERIALS
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Supplementary Text
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22 June 2017; accepted 25 September 2017
Published online 5 October 2017
10.1126/science.aao1807

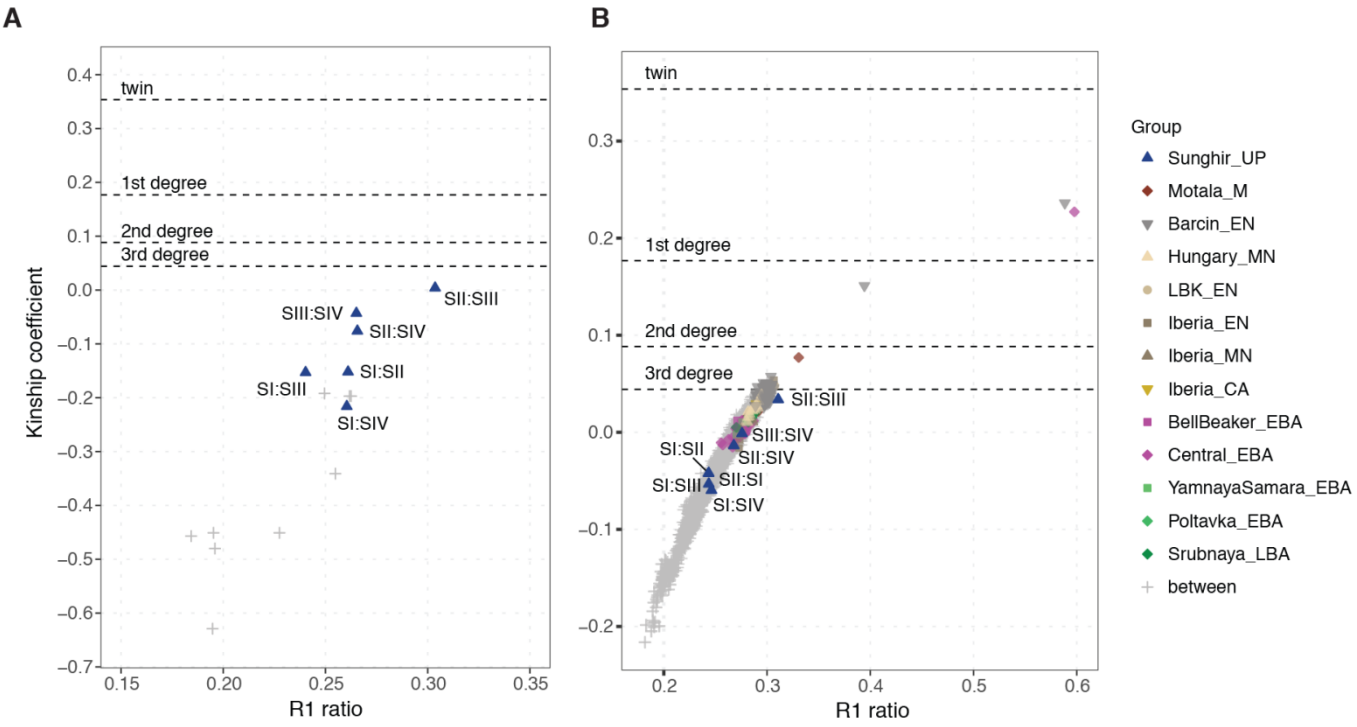

Fig. 1. Relatedness among ancient Eurasians. Kinship coefficients and R1 ratios inferred from IBS ratios for (**A**) Pairs of UP individuals, using 1000 Genomes Phase 3 SNP sites. (**B**) Pairs of ancient Eurasians, using 1240K capture SNP sites. Within-group pairs of Sunghir are highlighted.

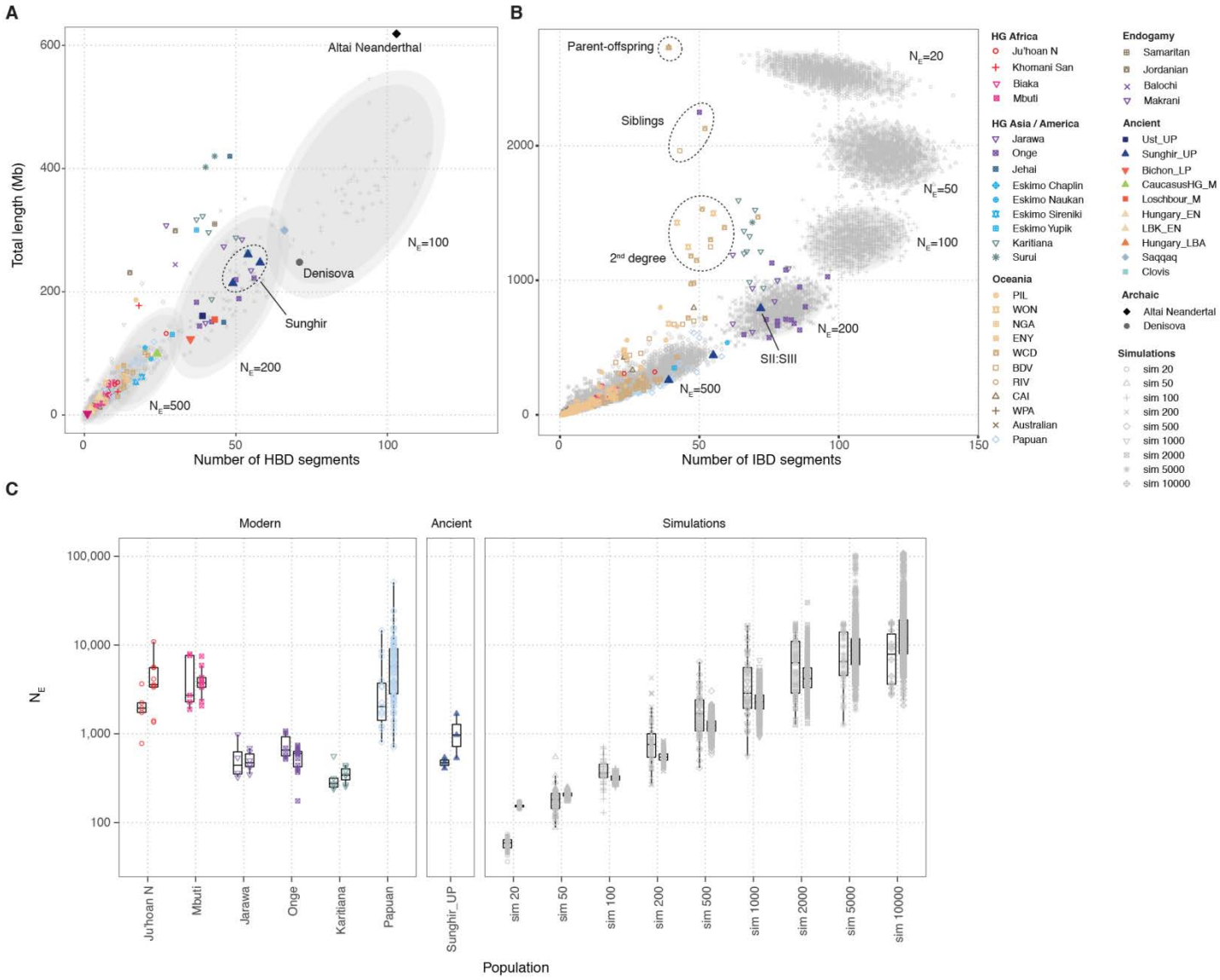

Fig. 2. Identity-by-descent and recent effective population sizes. (**A** and **B**) Distributions of the number and total length of HBD and IBD segments in modern, ancient and archaic humans (Altai Neandertal and Denisovan). Ellipses indicate 95th and 99th percentile of the distributions inferred from simulated data of various N_E values. Individuals with previously described close relatedness and their degree are indicated in (B). (**C**) Distributions of inferred recent effective population sizes for modern and ancient HGs with a minimum of three individuals, as well as simulated datasets of randomly mating populations with a range of N_E values. For each population, sizes inferred from HBD and IBD tracts are on the left and right side, respectively.

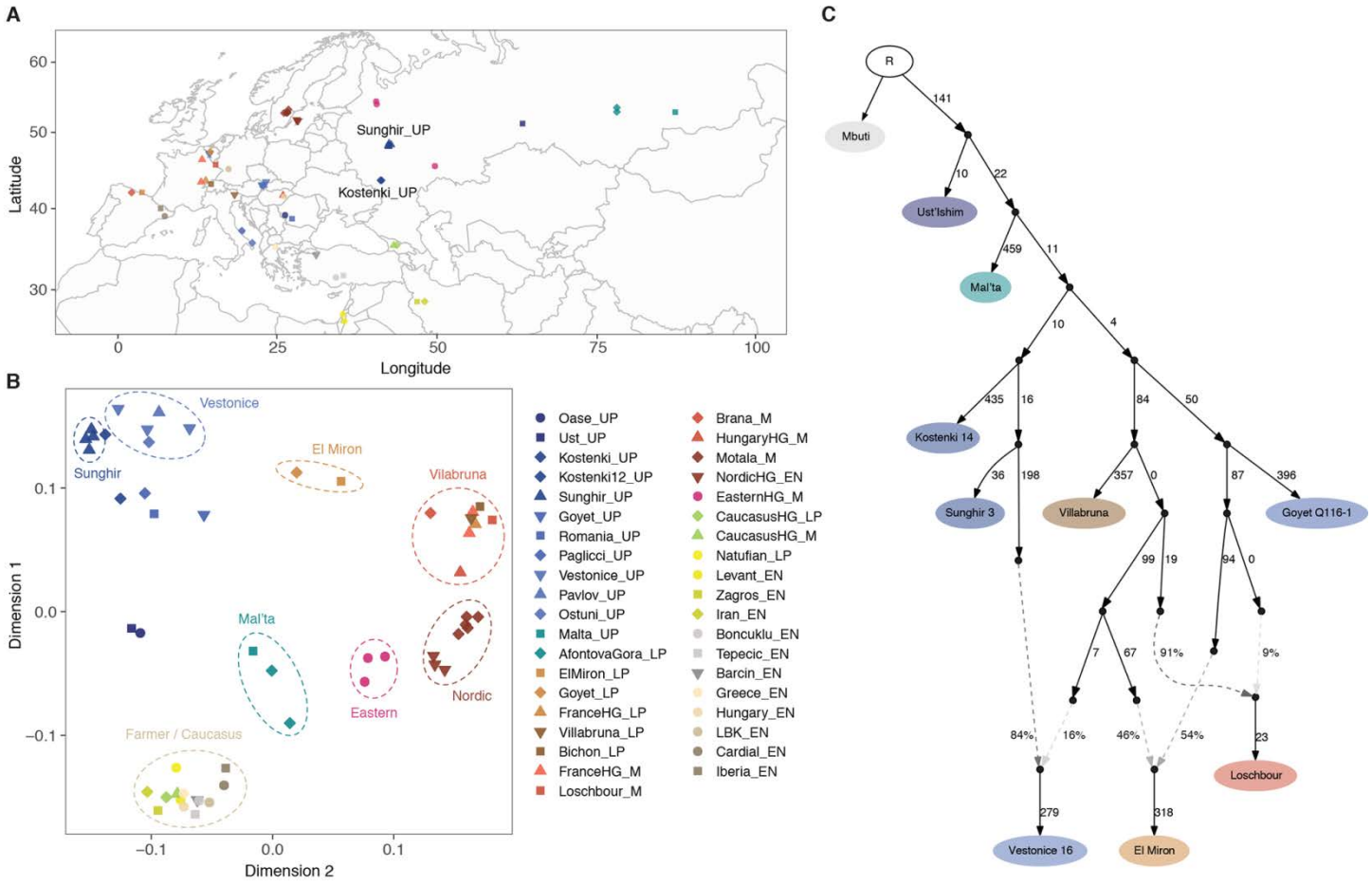

Fig. 3. Genetic affinities of the Sunghir individuals. (**A**) Geographic locations of ancient Eurasian individuals used in the analysis. (**B**) Multi-dimensional scaling of ancient individuals based on pairwise shared genetic drift (outgroup *f*3 statistics f_3(Mbuti; Ancient$_1$, Ancient$_2$)). (**C**) Admixture graph showing the best fit of Sunghir with other early Eurasians.

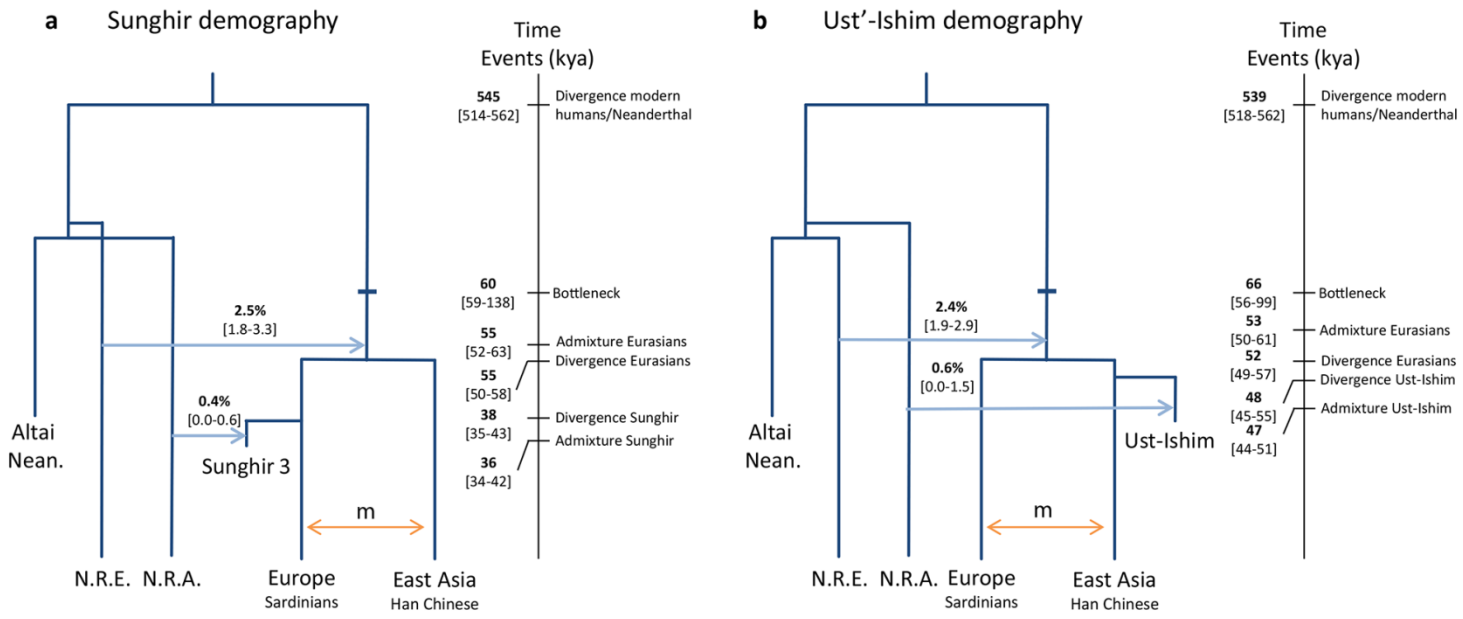

Fig. 4. Modelling of early Eurasian population history. Best-fit demographic models for early Eurasian admixture including (**A**) SIII and (**B**) Ust'-Ishim. Point estimates are shown in bold, and 95% confidence intervals are shown within square brackets. Times of divergence in years are obtained assuming a generation time of 29 years and a mutation rate of 1.25e-8/gen/site. N.R.E.: Altai Neanderthal-related ghost population contributing to Eurasians. N.R.A.: Altai Neanderthal-related ghost population contributing to ancient modern humans. Divergence of SIII from proto-Europeans was supported in 100/100 bootstrap replicates, whereas divergence of Ust'-Ishim from proto-Asians was supported in 99/100 bootstrap replicates.

Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers

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published online October 5, 2017

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.